Role of Wild Grasses in Epidemics of Powdery Mildew on Small Grains in Israel

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ABSTRACT

Three hundred and twenty-three conidial isolates of *Erysiphe graminis* from about 40 species of 16 genera of native wild Gramineae collected throughout Israel were used to inoculate seedlings of cultivated barley, wheat, and oats, grown in the greenhouse. Similar tests were made with 152 collections of fertile cleistothecia of *E. graminis* obtained from 26 species of 12 genera of grasses. Fungal isolates infectious on the small grains originated almost exclusively from intrageneric grasses, mainly from allied species. One exception was that conidia and ascospores from *Triticum dicoccoides* were compatible with cultivated wheat and barley. This specialization of *E. graminis* on grasses contrasts sharply with the broad host ranges of isolates from cereals. Despite the limited number of species which harbor pathogens infectious on small grains, they are important in the epidemics of powdery mildew because of their wide distribution and the seasonal coordination of their life cycles with that of the pathogen. Those grasses are infected in the fall by primary ascosporic inoculum liberated from cleistothecia which oversummer on their stubble. After infection, the conidia multiply and disseminate to cultivated small grain crops throughout the growing season. Cleistothecia preserved on the grass refuse enable oversummering of the fungus in the absence of live hosts.

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Barley, wheat, and oats (small grains) crops in Israel are generally susceptible to the powdery mildew fungi. The powdery mildew disease of wheat was not of economic significance until the increase in cultivation of semi-dwarf Mexican spring wheat cultivars and their local hybrids which are susceptible to powdery mildew abroad (3), and in Israel.

Wild Gramineae are very abundant and widely distributed in Israel. The importance of wild grasses in the epidemiology of stem rust of small grains has been demonstrated (7). Our previous greenhouse study (5) showed that *E. graminis tritici, E. graminis hordei,* and *E. graminis avenae* each possesses a wide host range among native grasses. The present study was undertaken to determine the role of wild grasses in the perpetuation and dissemination of powdery mildew fungi which attack small grains. Hardison (9) inferred that "wild grasses must now be considered in the epiphytology of the disease on cereals as sources of primary infection and perennial stations for the fungus". Other researchers (19) have concluded that in nature, powdery mildew of cultivated grasses are hardly capable of infecting small grain crops, and vice versa.

The formation, fertility, and longevity of cleistothecia on wild grasses, and the infectivity of their ascospores were investigated, because of the importance of the sexual stage in the survival of *E. graminis* over the hot, dry summer (2, 4, 8, 20, 21).

MATERIALS AND METHODS.—Conidia and cleistothecia were collected from indigenous wild grasses naturally infected by *E. graminis*.

Conidial tests.—The conidial specimens were collected during weekly or biweekly countrywide field surveys conducted from December through April. Some specimens were collected from the same locations at different times. A few cultures were obtained from native grasses tested in field nurseries situated near heavily mildewed barley and oat fields.

Grass plants with well developed powdery mildew pustules were lifted from the ground with their roots, placed in plastic bags and transplanted in garden pots in the greenhouse. The plants were isolated for 5-7 days in glass chimneys or plastic cylinders with filter paper covers to eliminate conidia which might have been on the plants but did not cause infection. Such conidia retain viability for no more than 4 days (5, 8). After the isolation period, the conidia were transferred with a camel's hair brush from the host plant to uninfected seedlings of the barley cultivar 'Manchuria' (C.I. 2330), vulgare wheat 'Florence × Aurore' (known as F.A. 8193), durum wheat 'Oued-Zenati × Boutaille' (ordinarily referred to as Z.B.), and oat cultivars 'Fulghum' or 'Mulga' which are susceptible to powdery mildew in the fields. The grass plants were grown to maturity outdoors with sufficient irrigation. Their inflorescences enable taxonomic identification, and their seed was used for reinfection in seedling experiments.

The seedlings were protected in all inoculation experiments from chance contamination by growing them in pots under glass chimneys tightly covered with filter paper caps.

Seedlings produced from seed of the grass plants were inoculated with cultures of *E. graminis* isolated from artificially infected seedlings of the wheat, barley, or oat cultivars maintained in a series of reisolation and reinoculation cycles. The procedure was modified when the identity of the wild grass was known. In such cases, seedlings in reinoculation tests were produced from seed harvested in previous years from plants of the same species. Seeds were collected in nature in the vicinity of the source host or harvested from plants which had proven to be susceptible to powdery mildew in preceding

TABLE 1. Fertility of cleistothecia of *Erysiphe graminis* DC. from different wild grasses and the infectivity of their ascospores to plants of the respective source species

	Cleistothecia from potted grasses		Cleistothecia collected in nature	
Source species	Rate of fertility	Cleistothecia with infectious ascospores	Rate of fertility	Cleistothecia with infectious ascospores
Aegilops				
peregrina	2/10[a]	1	4/5[a]	1
speltoides	...	...	5/5	1
sp.	1/2	0	...	...
Avena				
barbata	0/1	...	3/7	0
sterilis	3/6	1	9/21	5
Bromus				
aegyptiacus	...	...	1/1	1
alopecurus	3/4	3	1/1	0
japonicus	1/1	1	...	...
lanceolatus	1/1	1	1/3	0
madritensis	4/4	1	1/1	0
rigens	1/1	1	2/2	2
scoparius	2/4	2	...	...
Cutandia				
philistea	0/1	...	...	...
Cynosurus				
echinatus	1/1	0	...	...
Dactylis				
glomerata	0/1	...	1/1	1
Hordeum				
bulbosum	8/13	6	8/8	8
marinum	2/2	1	6/7	6
murinum (+ *leporinum*)	24/26	24	5/6	5
spontaneum	...	...	5/7	5
Koeleria				
phleoides	...	...	1/1	0
Lepturus				
cylindricus	2/2	0	...	...
Lolium				
rigidum	2/2	0	0/1	...
sp.	...	...	2/2	0
Phalaris				
brachystachys	1/1	1	2/2	1
bulbosa	1/2	1	...	...
minor	3/4	3	1/1	1
paradoxa	6/9	2	4/4	4
Scleropoa				
rigida	2/2	0	10/10	6
Triticum				
dicoccoides	3/6	1	7/7	7

[a]Numerator designates the number of collections with fertile cleistothecia; the denominator refers to the total number of collections tested. In each collection, 10-20 cleistothecia were examined, after exposure in closed petri dishes for 72 hours or more at 20 ± 2 C under high humidity.

trials or field surveys. Cultures were classed as compatible with the respective small grain, only when isolates from the latter host reinfected grasses of the source species.

Ascospore tests.—One-hundred-six straw specimens bearing cleistothecia were collected from stubble of potted grass plants grown outdoors. Conidia tested in the seedling trials described above were collected from the same plants prior to transplanting. Another 103 samples of cleistothecia were obtained from dry grasses collected in countrywide field surveys during June and July. The plants with inflorescences were collected in paper bags and brought to the laboratory for inoculation studies and identification of the hosts. Straw pieces bearing cleistothecia were maintained in closed petri dishes lined with moist filter paper at 20 ± 2 C for at least 72 hours to induce ascospore formation (5). Fertility of cleistothecia was assayed by microscopic examination of 10-20 fruiting bodies in each straw sample. About seven days earlier,

TABLE 2. Infectivity of *Erysiphe graminis* from wild grasses on seedlings of cultivated barley, oats, and wheat in the greenhouse at 20 ± 2 C

Inoculum source host	Type of inoculum and its origin				Seedling infection in			
	Conidia isolated from grasses in		Ascospores from cleistothecia produced		barley	oats	wheat	
	test nursery	nature[a]	on potted plants[a]	on grasses in nature			Z.B.[e]	F.A.[f] 8193
Avena								
barbata		+				4/8[b] (1/8)[c]		
	+					1/1		
longiglumis		+				(1/1)		
	+					1/1		
sterilis		+				12/24 (4/24)		
	+					1/1		
			+			0/1		
				+		2/5		
wiestii		+				7/9 (2/9)		
	+					1/1		
sp.		+				1/1		
Hordeum								
bulbosum		+			(1/20)			
			+		1/6			
				+	2/8			
marinum		+			0/8			
	+				0/1			
			+		0/1			
				+	3/6			
murinum (+ *leporinum*)		+			5/53 (19/53)			
	+				0/1			
			+		13/24			
				+	2/5			
spontaneum		+			9/27 16/27[d]			
	+				1/1			
				+	5/5			
Koeleria								
phleoides	+					1/1		
Phalaris								
sp.		+				(1/33)		
Trisetum								
koelerioides	+					1/4 (1/4) 2/4		
lineare	+					(1/2) 1/2		
Triticum								
dicoccoides		+			1/7 (1/7)		5/8 (1/8)	0/8
			+		1/1		1/1	0/1
				+	2/7		7/7	0/7

[a]Conidia in nature and ascospores on potted plants were collected from the same hosts, at the green stage and the ripe stage, respectively.

[b]Denominator indicates the total number of inoculum samples tested; numerator designates the number of inoculum samples which induced on respective crop plants formation of conidia infectious on the source grass.

[c]In parentheses, numerator refers to the number of inoculum samples which induced on the crop plant formation of conidia noninfectious on the source grass.

[d]In underscored fractions, numerator denotes the number of inoculum samples infectious on the respective plant. However, no attempts were made to reinfect the source grass with conidia from the cereal plant.

[e]Durum wheat cultivar, Oued-Zenati × Boutaille.

[f]Vulgare wheat cultivar, Florence × Aurore.

barley, wheat, and oats were sown in garden pots. Seeds of the plants, from which the cleistothecia used to supply inoculum were obtained, were planted in the center of each pot. Whenever seed of the cleistothecia-bearing plant could not be obtained, seeds of intraspecific grasses susceptible to *E. graminis*, as determined by previous tests, were used. The planting of seeds was staggered so that all seedlings were at nearly the same stage of development when inoculated. The seedlings were isolated in glass chimneys covered with filter paper caps. The caps were replaced by inverted bottoms of petri dishes lined with segments of the grass plant with fertile cleistothecia. After exposure for a minimum of 72 hours at 20 ± 2 C, at high humidity, filter paper covers were substituted for petri dishes. We assumed that seedling infection was incited by ascospores (5). We have failed to obtain viable conidia from straw of grasses or small grains brought from the fields in the summer. Inoculum infecting the small grain seedlings as well as grass seedlings in the same pot, was considered to be congenial with the small grain.

In both the conidial and ascospore inoculation tests, readings were taken at least twice, at 10 and 14-16 days after inoculation.

RESULTS.—*Formation and fertility of cleistothecia.*—Fruiting bodies were consistently recorded on *Phalaris* and *Hordeum* (Table 1). In contrast, cleistothecia were relatively rare on *Avena* and even more scarce on *Lolium* sp. The intensity of cleistothecium development on some grasses fluctuated from one year to another. Cleistothecia developed profusely on oats in the grass nursery in 1964, but could not be found the ensuing year. These results corroborate those reported in other countries that production of cleistothecia is dependent on climatic conditions (2, 4), the genotype of the fungus, and the host (2). Turner (22) emphasized that cleistothecia are less frequent on oats than on wheat and barley.

The data in Table 1 reveal that ascospores form in cleistothecia on numerous grasses following the treatment described in the section on Materials and Methods. Fruiting bodies produced on various host genera or even species differ in their fertility.

Ascospore infectivity on grasses.—The infectivity of ascospores formed in cleistothecia of the grasses investigated (Table 1) differed on the progenies of the source hosts or their relatives which were susceptible to powdery mildew. This phenomenon can be attributed to the genetic variability of the pathogen (2) and the wild grasses. A single plant of *Hordeum spontaneum* yielded progenies resistant and susceptible to the same inoculum (Sobel and Wahl, *unpublished*). One test plant of *Aegilops speltoides* produced seedlings resistant to powdery mildew cultures virulent on the parent plant.

Reaction of small grains to powdery mildew from grasses.—Seedlings of barley, wheat, and oats were inoculated with 323 conidial isolates obtained from wild grasses in natural habitats and with 17 isolates from wild grasses grown in test nurseries. Similar trials were carried out with ascosporic inocula from 79 samples of fertile cleistothecia secured from dry grasses in nature and 73 samples obtained from grasses grown in garden pots following transplanting from nature. Inoculum isolated from successfully infected small grain seedlings was used for infecting progenies of the source grass host, or their relatives whose parents displayed susceptibility to powdery mildew in previous trials. Some attempts to reinfect grass hosts resulted in failure, especially when conidia derived from the small grain plants were isolated from thin, indefinite pustules with scanty mycelium and conidiophores, symptomatic of "subinfection".

None of the conidial isolates obtained from the following grass species (the numbers which follow each species named below designate the number of isolates obtained from that species) was infectious on the small grain seedlings: *Aegilops crassa* Boiss., 1; *Ae. longissima* Schw. & Muschl., 1; *Ae. peregrina* (Hack.) Eig, 18; *Ae. speltoides* Tausch, 3; *Alopecurus myosuroides* Huds., 3; *Bromus alopecurus* Poir., 14; *B. fasciculatus* Presl., 1; *B. japonicus* Thbg., 1; *B. lanceolatus* Roth., 6; *B. madritensis* L., 15; *B. rigens* L., 7; *B. scoparius* L., 4; *B.* sp., 4; *Cynosurus echinatus* L., 2; *Dactylis glomerata* L., 5; *Eremopyrum buonapartis* (Spreng.) Nevski, 1; *Lamarckia aurea* (L.) Moench., 2; *Lepturus cylindricus* (Willd.) Trin., 4; *Lolium gaudini* Parl., 3; *L. rigidum* Gaud., 23; *L. temulentum* L., 1; *L.* sp., 7; *Phalaris brachystachys* Lk., 2; *P. bulbosa* L., 2; *P. minor* Retz., 15; *P. paradoxa* L., 13; *Scleropoa rigida* (L.) Griesb., 4. Negative results also were obtained when cultivated barley, wheat, and oats were inoculated with ascospores derived from the listed grasses, although ascospores of the same origin were infectious on plants of the source host species (Table 1). Data concerning the origin of powdery mildew isolates infectious on small grains are summarized in Table 2.

Hordeum spontaneum C. Koch, the putative ancestor of *H. sativum* Jess., is distributed throughout Israel (10). Powdery mildew isolates obtained from this species, from the Galilee in the north to the Negev in the south, produced conidia on cultivated barley infectious on the source host. Such cultures were less common on *H. murinum* L. (including *H. leporinum* Link), and rare on *H. marinum* Huds. and *H. bulbosum* L. (in Israel, 2n = 28). On the latter two species, cultures compatible with cultivated barley were of ascospore origin. *H. spontaneum,* because of its wide distribution, is important in initiating and disseminating inoculum virulent on barley crops (6).

Wild oats are very prominent native grasses. The hexaploid *Avena sterilis* L. and the tetraploid *A. barbata* Pott. are ubiquitous, and often constitute the predominant component of the annual herbaceous cover in winter and spring (13). The diploid psammophyte *A. longiglumis* Dur. appears sporadically in various regions, and the diploid *A. wiestii* Steud. is a desert type. Maps showing the distribution of these species in Israel were published (13). Cultivated oats were receptive to about 50 percent of conidial isolates sampled from *A. sterilis* and *A. barbata* and supported development of inoculum infectious on the source hosts. Likewise, *A. sativa* was susceptible to conidial isolates from *A. longiglumis* and *A. wiestii.* Obviously, wild oats are important for the increase and spread of powdery mildew inoculum virulent on cultivated oats.

The tetraploid wild emmer *Triticum dicoccoides* Koern. is abundant in the Eastern Galilee, being less common in other regions. Only preliminary studies were made on the reaction of cultivated wheat to isolates from *T. dicoccoides.* The conidial and ascosporic isolates were procured mainly from one location. Some of the isolates were virulent on the durum cultivar 'Z.B'., and developed conidia infectious on the source grass. These isolates were also parasitic on the vulgare cultivar 'Rescue', but noninfectious on the bread wheat F.A. 8193 and the semi-dwarf cultivars of Mexican descent, which are susceptible in the fields. One conidial isolate and three ascosporic isolates obtained from *T. dicoccoides* infected seedlings of cultivated barley, producing flat indefinite pustules with conidia infectious on the wild emmer. Cultures combining compatibility with wheat and barley have remained stable for over 10 years. During this period they were involved in more than 100 reinoculation and reisolation cycles on durum wheat.

The infectivity of conidial isolates obtained from 50 grass hosts of the genera *Avena, Hordeum,* and *Triticum* was compared with isolates obtained from ascospores on the same plants in garden pots (Table 2). Preliminary results indicate that the parasitic properties of the conidial isolates and their ascospore counterparts are very similar. Insignificant differences were observed in a few cases. For example, ascospores from wild *Hordeum* and *T. dicoccoides* appeared to be somewhat more infectious than conidia from the same source. Our previous investigations (5) and studies in other countries "indicated equal infective powers of ascospores and conidia" (24).

The results obtained by us show that small grains became infected mainly with powdery mildew from intrageneric grasses, and primarily from allied species. In a few instances inoculum derived from other genera was successfully transferred to small grains. In addition to the mentioned passage of powdery mildew from *T. dicoccoides* to barley, cultivated oats were infected with inoculum from *Trisetum koelerioides* Bornm. et Hack., and probably also with isolates from *T. lineare* (Forsk.) Boiss. and *Koeleria phleoides* (Vill.) Pers., all belonging to the tribe Aveneae. In the last two instances, the pathogen was not transferred to the source hosts (Table 2). Infection of cereal crops with *E. graminis* isolated from outside the respective genera of grasses has also been reported in other countries (9, 17, 18).

Longevity of cleistothecia.—Cleistothecia of *E. graminis* have been reported to remain fertile for several years (8, 15). We determined whether cleistothecia on wild grasses remain functional during the summer season when maintained at room temperatures, which are often above 30 C. The results showed that under those conditions, cleistothecia carried on stubble of the following grasses yielded ascospores infectious to the source hosts after the number of days indicated after each name: *Aegilops peregrina,* 202; *Avena sterilis,* 248; *Bromus aegyptiacus,* 190; *B. lanceolatus,* 223; *Hordeum bulbosum,* 205; *H. marinum,* 227; *H. murinum,* 222; *H. spontaneum,* 207; *Koeleria phleoides,* 193; *Lepturus cylindricus,* 192; *Lolium rigidum,* 221; *Phalaris paradoxa,* 326; *Scleropoa rigida,* 244; and *T. dicoccoides,* 176. The longevity of cleistothecia outlasts the summer period even in unfavorable environments.

Oversummering of E. graminis.—Small grains are grown in Israel in the rainy season, from mid-October through May. The life cycle of winter grasses, including those harboring powdery mildews infectious on barley, wheat, and oats, parallels that of cereal crops. With the advent of the rainless and hot summer these grasses dry up except in small irrigated sites. Volunteer plants also overseason occasionally at such sites.

The conidial stage remained viable over the summer on live potted plants of *Aegilops, Avena, Lolium, Phalaris,* and *Trisetum* species maintained in shady places and sufficiently watered. So far, only representatives of these genera have been investigated. In nature, viable conidial pustules were found throughout the summer in a few instances on live plants of *Avena barbata* and *Hordeum bulbosum* in relatively cool places at high elevations in the Galilee. Oversummering of conidia under natural conditions is rare and of no epidemiological significance in Israel. Nor is the mycelium capable of tiding the fungus over the summer (12).

The importance of cleistothecia in ensuring the survival of *E. graminis* during the dry summer has been emphasized in Serbia (21), Southern Italy (20), the U.S.S.R. (8) and Canada (4). According to Blumer (2), cleistothecia on stubble of wheat and barley in the fields of Central Europe liberate ascospores with the first rains in fall and infect small grains sown in that season, volunteer cereals, and possibly also grasses. In Israel, cleistothecia are the principal means of oversummering of *E. graminis hordei,* and ascospores discharged at the onset of the rainy season infect wild and cultivated barley (12). Similar results were obtained in our studies with *E. graminis avenae.* Ascospores formed and ejected at the beginning of the rainy period infect seedlings of wild oats emerging across the country, and occasionally volunteer oats, prior to the appearance of the disease on oats crops. Conidia produced as a result of these infections are distributed to cultivated fields. The process of ascospore release and seedling infection was reproduced in the greenhouse under controlled conditions. Seedlings of *Triticum dicoccoides* infected with powdery mildew have been detected in the fall near the stubble of this grass harboring cleistothecia with infectious ascospores. They formed the initial foci of conidia virulent on durum wheat. Their potential threat to barley cultivars cannot be disregarded. Also, infection of plants belonging to *Aegilops, Bromus, Phalaris* species, and *Scleropoa rigida* in the fall is very likely started by ascospores released from cleistothecia borne on debris of the respective grasses. The fertility of such cleistothecia, and the infectivity of their ascospores to the host plants, also has been demonstrated in greenhouse trials.

DISCUSSION AND CONCLUSIONS.—Our previous studies (5) demonstrated that isolates of *E. graminis hordei, E. graminis tritici,* and *E. graminis avenae* obtained from the respective cultivated hosts were compatible with wild grasses belonging to different genera in several tribes. In the present study, seedlings of barley, wheat, and oats were congenial almost exclusively with isolates derived from intrageneric grasses, and mainly from related species. Bawden (1) postulated that in genetically heterogenic populations in "wild" habitats, "each plant is a selective ecologic niche favoring only a few parasites". The specialized host-parasite relationship in the *E. graminis* - wild grasses system in nature supports Bawden's hypothesis. Meiners (14), on the basis of studies with *Tilletia caries,* suggested that "possibly many species may have some type of natural barrier ... which is broken down by inoculation procedure". A similar breakdown of barriers may have taken place when seedlings on wild grasses were artificially inoculated with powdery mildew from small grains. However, this procedure may not be sufficient to invalidate the host specificity of fungal strains that have evolved on native grasses.

Erysiphaceae are considered to be less-specialized parasites than rusts (2). This conclusion does not seem to apply to *E. graminis*. Gerechter-Amitai (7) showed that grasses of numerous genera harbor stem rust prevalent on small grains and reciprocal interchange of inoculum is common. The situation of *E. graminis* is different. None of the isolates from *Aegilops* species was infectious on wheat, while stem rust from these grasses was readily transferred to wheat. Data of the present study support the retaining of the varietal subdivision of *E. graminis* (5, 9).

The common occurrence of the functional sexual stage in *E. graminis* conceivably results in development of intervarietal hybrids which blend the parasitic properties of the parental varieties. "The relative simplicity of the barrier separating the *formae speciales*" (23) enables their intercrossing. This process might have been responsible for the evolution of powdery mildew on *T. dicoccoides* compatible with cultivated wheat and barley. Intervarietal hybrids in *E. graminis* are expected to behave like their counterparts in small grain rusts (11), and to be less common in nature and less adaptive to small grains than the typical *tritici* and *hordei* cultures. Passage of powdery mildew from wheat to cultivated barley has never been successful, except when predisposition treatment was employed (16).

Some of the wild grasses with powdery mildew infectious on small grains are of countrywide occurrence, and are important in the dissemination of the pathogen. Cleistothecia carried on the stubble of these grasses are the principal means of oversummering of the fungus and produce ascosporic inoculum in the fall which initiates disease development.

The commonness of fertile cleistothecia on native grasses is presumably an outcome of natural selection. The cleistothecia enhance the survivability of *E. graminis* in semi-arid regions. This situation is at variance with the concept of the "non-necessity" of cleistothecia (24) and with the tendency for their suppression on grasses with a long vegetative growth period (8).

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